New Phytologist

Commentary

The limits to leaf and root plasticity: what is so special about specific root length?

Expectations

Plants can adjust to their environment at various integration levels: they may change the relative investment of biomass to leaves, stems and roots, they can alter the morphology and anatomy of each of these organs, or they can change the physiological characteristics of the cells that form these organs. Most likely, they adjust at all three levels. It would be a major achievement if we understood quantitatively the functional contribution of each of the adjustments and how they interact with each other. In this issue of *New Phytologist*, Freschet *et al.* (pp. 1247–1260) tackle the relative importance of acclimation at the level of allocation and morphology, and seek to determine how plants respond if they are challenged with low or high light levels in combination with a low or high supply of nutrients.

'Freschet et al. *are the first to show this in such an elegant way, and across so many functionally different species.'*

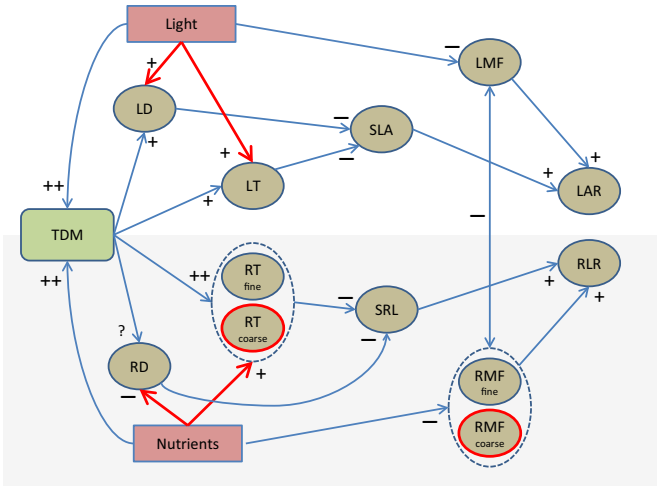
Allocation can be quantified as the fraction of biomass invested in leaves (LMF, leaf mass fraction), stems (SMF, stem mass fraction) and roots (RMF, root mass fraction; see Fig. 1 for explanations). Morphology can be expressed in terms of total leaf area per unit leaf mass (SLA, specific leaf area), the length of stem per unit stem mass (SSL, specific stem length) or the total length of root per unit root mass (SRL, specific root length). Based on generalized dose–response curves, Poorter *et al.* (2012) found that in response to most abiotic environmental variables, proportional changes in LMF were much smaller than changes in leaf morphology. This was also true for the plasticity in SMF relative to variability in stem morphology in response to plant density. A relatively low plasticity in allocation seems plausible since most plants always need a minimum amount of leaves, stems and roots to function properly. Variation in morphology seems less constrained. Based on these considerations and observations, Poorter *et al.* (2012) suggested that plants generally have more flexibility to alter their morphology than their biomass allocation.

Observations

Freschet *et al.* challenged plants with two contrasting environmental factors: the amount of light supplied to the shoots and the amount of nutrients supplied to the roots. Following expectations, plants grown at low light partly responded by increasing leaf area per unit total plant mass, to some extent by increasing LMF, but predominantly (~70%) by increasing SLA (Fig. 2a). In this way, they increased the leaf area per unit plant mass at low light, and thereby the interception of photons. Interestingly, this was *not* mirrored by similar changes belowground when nutrients were decreased. Although SRL was to some extent enhanced by low nutrients, the relative stimulation in RMF turned out to be far more important than the relative change in SRL in increasing total root length per unit plant mass (RLR, root length ratio; Fig. 2b). Freschet *et al.* are the first to show this in such an elegant way, and across so many functionally different species. In a range of previous experiments that only targeted nutrient supply, the relative changes in SRL were even smaller than in the current experiment (Fig. 2b). Altogether, these experiments provide a rather consistent picture, which shows that with nutrient stress the increased allocation to roots seems more important for the plant to achieve an increase in root length than the change in root morphology. These results help us to better understand whole-plant responses to the environment and the expectation of high plasticity in root morphology can be dismissed. At the same time, these findings raise a range of interesting subsequent questions, of which we will discuss four.

Subsequent questions

One of the most intriguing questions raised by Freschet *et al.*'s work is why SRL shows so little response to changes in nutrient availability. Would a high SRL not improve the overall nutrient uptake rate? An important contrast between leaves and roots is that the latter are not 'simply' the terminal parts attached to stems and branches and their task is not only to take up nutrients and water. The root system is a continuously expanding organ. Moreover, it also has to provide anchorage and transport, which requires a certain amount of support and transport tissue. To better understand root functioning, we therefore have to conceptually separate the parts of the roots that serve those different functions (Eissenstat *et al.*, 2000). Overall low nutrient levels have been observed to have a positive effect on the SRL of the finest roots, which are responsible for resource acquisition (Ostonen *et al.*, 2007). However, locally present nutrient-rich soil patches will increase the number and extension rate of fine lateral roots, which has a positive effect on overall SRL, be it that those laterals have a 2–3-times greater diameter than laterals in low-nutrient patches, which in turn will have a negative effect (Drew *et al.*, 1973). Hence, as the total root system reflects various tasks and different tissues, we



Abbreviation	Explanation	Definition	Units
LMF	Leaf mass fraction	leaf mass/plant mass	g g^{-1}
SMF	Stem mass fraction	stem mass/plant mass	g g^{-1}
RMF	Root mass fraction	root mass/plant mass	g g^{-1}
SLA	Specific leaf area	leaf area/leaf mass	m^2 kg^{-1}
SSL	Specific stem length	stem length/stem mass	m g^{-1}
SRL	Specific root length	root length/root mass	m g^{-1}
LD	Leaf density	leaf mass/leaf volume	g ml^{-1}
LT	Leaf thickness	leaf volume/leaf area	ml m^{-2}
LAR	Leaf area ratio	leaf area/plant mass	m^2 kg^{-1}
RD	Root density	root mass/root volume	g ml^{-1}
RT	Root thickness	root volume/root length	ml m^{-1}
RLR	Root length ratio	root length/plant mass	m g^{-1}
TDM	Total dry mass	plant mass	g

Fig. 1 Scheme representing the effect of light and nutrient availability on the various variables discussed in this Commentary. +, −, indicate positive and negative effects, respectively. In the case of the actors with more effects, the strongest effect is indicated with ++. Red lines indicate differences between roots and leaves, which potentially cause different responses of SLA and SRL to resource availability: responses of the components of SLA act in a synergistic manner, while those of SRL are antagonistic. Nutrient and size effects on RMF and RT will be influenced by differential responses of fine and coarse roots. For clarity we omitted several effects, including the positive effect of low light on SRL.

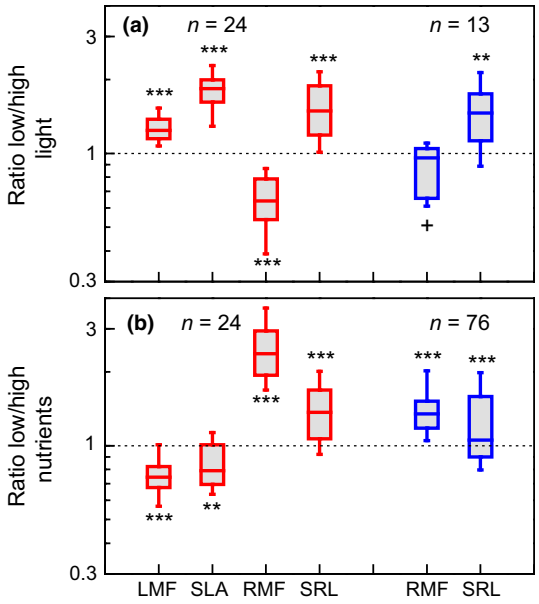


Fig. 2 Box plots indicating the range of responses between (a) low-light and high-light grown plants and (b) low-nutrient and high-nutrient grown plants. The red data summarize the values of Freschet *et al.* (in this issue of *New Phytologist*, pp. 1247–1260), the blue ones are a compilation taken from the literature. The boxes indicate the 25th and 75th percentile of the distribution, the 'whiskers' the 10th and 90th percentile and the lines in the middle of the box the median value. Numbers indicate the number of observations on which the boxplots are based. Asterisks indicate significant deviations from unity: +, $0.05 < P < 0.10$; **, $P < 0.01$; ***, $P < 0.001$. (a) Data from: van Hees (1997); Ryser & Eek (2000); Bloor (2003); Curt *et al.* (2005). (b) Data from: Boot & den Dubbelden (1990); Boot & Mensink (1990); Aerts *et al.* (1992); Elberse & Berendse (1993); Pettersson *et al.* (1993); Ryser & Lambers (1995); Schippers & Olff (2000); Nagel *et al.* (2001); Sigurdsson *et al.* (2001); Reich *et al.* (2003).

may expect the nutrient effect on overall root morphology to be more modest than that of light on leaf morphology (Fig. 1). Of additional importance is the aspect of allometry. SLA is somewhat affected by plant size, but the effect on SRL is generally much stronger (Ryser & Eek, 2000). The reason for this is because plant root systems will necessarily expand more in mass than in length to maintain transport capacity and stability. This is one of the reasons why separation into coarse and fine roots for trees is common practice (Pregitzer *et al.*, 1997). Freschet *et al.* – like most researchers in this field – harvested their plants at similar ages. As the plant's biomass in their experiment differed up to 10-fold in size between treatments it would be well worth studying the allometry of the relationship between root mass and length in greater detail. Even better would be to characterize the overall distribution of SRL over the whole root system, rather than just study the average SRL of the plants.

A second question relates to cellular/biochemical aspects. Both SLA and SRL are composite traits, and depend on organ thickness and tissue density (Fig. 1; Ryser & Lambers, 1995). For leaves, light limitation generally leads to a reduction in both thickness and density (Poorter *et al.*, 2009). Similarly, roots generally respond to decreasing nutrient availability by becoming thinner (Zobel *et al.*, 2007), but in contrast to the effect of light limitation on leaves, available data suggest that root tissue density *increases* with decreasing nutrients (Ryser & Lambers, 1995; Trubat *et al.*, 2012). Consequently, the response of SRL to low nutrients is far less consistent than that of SLA to low light (Fig. 1). We would therefore profit from more insight into the anatomical and biochemical basis of environmentally-induced variation in root density.

A third issue is that acclimation will act on various aspects of plant performance simultaneously, with positive effects possibly counterbalanced by other influences. In shaded leaves, for example, the increase in SLA will improve the capture of limiting photons, but may also lead to increased vulnerability to herbivores, the selected adaptive response being a compromise (Salgado-Luarte & Gianoli, 2011). By the same token, higher nutrient supply does not reduce biomass allocation to roots in shrubs in xeric environments, where a reduced root mass would increase vulnerability to drought (Trubat *et al.*, 2012). That study also describes how an increase in SRL at low nutrient availability requires a reduction in leaf area to ensure hydraulic safety when root hydraulic conductance diminishes with increasing SRL. It would be interesting to achieve more insight into these internal trade-offs within the plant. To what extent the plant benefits from the increased SRL in terms of

additional nutrient uptake, and to what extent this differs between different types of nutrient (nitrogen, phosphorus, potassium), is also still a matter of debate (Zobel *et al.*, 2007). Similarly, what are the consequences of these anatomical and biochemical changes for root longevity?

A fourth question triggered by the results of Freschet *et al.* and others relates to the relatively consistent increase of SRL with decreasing light (Fig. 2a). Is the higher SRL simply a consequence of low-light plants being smaller, possibly with less secondary growth (Reich *et al.*, 1998; Curt *et al.*, 2005), or is this a more complex response? In grasses, for example, it has been shown that shading increases xylem vessel diameter, possibly to ensure a sufficient hydraulic conductance of the reduced root mass to supply water for the leaves (Wahl *et al.*, 2001).

Outlook

The relative ease by which, for example, low-light responses of plants can be separated into physiological, morphological and allocation components can only be dreamt of by root researchers. Nevertheless, Freschet *et al.* were able to provide us with a clear view of various whole-plant responses and how special SRL was in that respect. Worthwhile next steps would be to follow up their results and deepen our insights into why the response of SRL is so modest as compared to root allocation. To properly understand the functional consequences of root responses for the uptake of nutrients and water, the difficult task of separating root mass into fractions that better correspond to its different functions may be essential. It is also important to continue experiments with an integrative whole-plant approach, including size effects and interacting selective pressures.

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